

Do Oystercatchers Influence Limpet Shell Shape?

by

P. A. R. HOCKEY¹ AND G. M. BRANCH²

¹ Percy FitzPatrick Institute of African Ornithology, University of Cape Town,
Rondebosch 7700, South Africa

² Department of Zoology, University of Cape Town,
Rondebosch 7700, South Africa

Abstract. The Black African Oystercatcher, *Haematopus moquini*, most often attacks limpets at the posterior margin. When feeding on *Patella granularis*, it preferentially attacks individuals that are pear-shaped rather than elliptical, presumably because the posterior margin is more easily distinguished in such shells. *Patella granularis* is more pear-shaped in habitats inaccessible to oystercatchers and in localities lacking oystercatchers, indicating that the selective effect of oystercatchers is sufficient to alter the phenotypic shell shape and probably also the genotypic composition of limpet populations preyed upon.

INTRODUCTION

VARIATIONS IN THE intensity of predation on gastropod populations by fish and invertebrates can lead to regional adaptations in shell morphology (EBLING *et al.*, 1964; VERMEIJ, 1978; PALMER, 1979), but very little is known about predation by birds in relation to shell form (VERMEIJ, 1978; but see HARTWICK, 1981) in spite of the fact that birds may have a substantial impact on limpet populations (FRANK, 1982).

Observations on shell remains lead to the conclusion that African Black Oystercatchers, *Haematopus moquini*, preferentially attack limpets (*Patella* spp.) at the posterior margin of the shell, and make "correct" attack decisions most consistently on limpet species whose posterior and anterior sectors are clearly distinguishable, such as *Patella cochlear* (HOCKEY, 1981). The dominant limpet in the diet of the African Black Oystercatcher is *P. granularis*, an elliptically shaped species of the mid- and upper-intertidal regions of southern Africa (Hockey & Underhill, MS). There is no specific orientation of *P. granularis* on rock faces (unpublished data); therefore, posterior attack is presumed to be choice by the birds. The proportions of attacks delivered by oystercatchers at the posterior, middle, and anterior sectors of the shells of this species are respectively, 49.3%, 12.1%, and 38.6% (n = 487) (HOCKEY, 1981).

Presumably, limpets that are approached from behind by oystercatchers have less warning of the attack and are, therefore, less likely to clamp down prior to attack. If African Black Oystercatchers are most successful when

attacking limpets posteriorly, it would be advantageous, when dealing with a uniformly elliptical species, to attack those individuals which are most pear-shaped, and hence have most recognizable posterior ends. If this strategy is adopted, then two testable hypotheses emerge concerning shell shape within populations of *P. granularis*.

Firstly, limpets in regions where there are no oystercatchers will be more pear-shaped than limpets in regions where oystercatchers occur, where pear-shaped limpets will have been removed preferentially.

Secondly, within regions where oystercatchers occur, limpets in inaccessible sites (vertical rock faces) will be more pear-shaped than accessible limpets, but, assuming genetic control of shell shape, more elliptical than limpets in areas where there are no oystercatchers.

METHODS

Random samples of *P. granularis* were collected at five localities in South Africa and Namibia within the range of the African Black Oystercatcher. Three types of limpets were distinguished: those eaten by oystercatchers (shells collected from chick "middens"); those living on rocks accessible to oystercatchers; and those living on rocks inaccessible to oystercatchers (vertical faces). Oystercatchers do not deposit all the shells that they remove in middens, but chick middens are the most reliable source of large quantities of shells that definitely have been preyed on by oystercatchers. Additionally, collections were made at sev-

Table 1

Mean shell uniformity indexes (SUIs) \pm SD for 17 samples of *Patella granularis* from southern Africa.

Type of limpet population	Sampling location	Mean length (mm) \pm SD	Mean SUI \pm SD
Depredated by oystercatchers	Malgas Is. (33°03'S; 17°55'E)	38 \pm 6	0.91 \pm 0.03
	Possession Is. (27°01'S; 15°12'E)	32 \pm 5	0.92 \pm 0.06
	Jutten Is. (33°05'S; 17°57'E)	45 \pm 11	0.92 \pm 0.04
	Overall mean		0.92 \pm 0.05
Accessible to oystercatchers	Malgas Is.	47 \pm 8	0.95 \pm 0.03
	Owen Is. (29°16'S; 16°52'E)	38 \pm 4	0.94 \pm 0.04
	Jutten Is.	36 \pm 5	0.93 \pm 0.03
	Cape Columbine (32°50'S; 17°50'E)	27 \pm 3	0.94 \pm 0.04
	Overall mean		0.94 \pm 0.04
Inaccessible to oystercatchers	Malgas Is.	36 \pm 5	0.92 \pm 0.04
	Jutten Is.	31 \pm 4	0.91 \pm 0.04
	Cape Columbine	24 \pm 3	0.93 \pm 0.06
	Overall mean		0.92 \pm 0.04
Predator-free	Swakop River (22°41'S; 14°31'E)	30 \pm 6	0.86 \pm 0.08
	Mile 105 (21°25'S; 13°50'E)	50 \pm 6	0.87 \pm 0.04
	Terrace Bay (20°00'S; 13°00'E)	31 \pm 6	0.93 \pm 0.03
	Mowe Bay (19°20'S; 12°43'E)	37 \pm 6	0.90 \pm 0.05
	Rocky Point (19°01'S; 12°29'E)	34 \pm 6	0.92 \pm 0.04
	Angra Fria (18°20'S; 11°58'E)	29 \pm 6	0.86 \pm 0.09
	Kunene River (17°20'S; 11°50'E)	50 \pm 7	0.88 \pm 0.07
	Overall mean		0.89 \pm 0.06

en sites in northern Namibia which are free from oystercatcher predation. Each sample comprised 30 individuals of various sizes, but the limpets selected for measurement fell within the size range eaten by oystercatchers (Hockey & Underhill, MS). All samples were taken from shores with high wave action.

For each limpet, a Shell Uniformity Index (SUI) was calculated. The SUI was the ratio of the width of the shell one third of the way from the anterior edge to the width one third of the way from the posterior edge: thus, individuals with SUIs close to unity were more elliptical than those with lower SUIs. Shell widths were measured with vernier calipers to the nearest 0.5 mm. For each sample a mean \pm SD was calculated, and mean SUIs were compared between samples using a t-test. Data (SUIs) were normalized using an arc sin transformation ($Y' = \sin^{-1}(\sqrt{Y})$) to allow statistical comparison. Limpet length (maximum, in mm) also was measured.

To test whether SUI is influenced by wave action independently of predation, two samples of 30 inaccessible limpets were collected at Froggy Pond (34°12'S; 18°28'E). One sample was taken from an area exposed to heavy wave action and the other from a sheltered area. These two samples contained a wide range of sizes and also were used to test whether SUI is related to size.

RESULTS

Shell Uniformity Indexes ranged from 0.86 ± 0.04 to 0.95 ± 0.03 (Table 1). T-tests indicated the following differences between populations of limpets in different regions and sites.

(a) The mean SUI for all limpets in predator-free populations (0.89 ± 0.06 , $n = 210$) was significantly less ($t = 6.89$, $P < 0.001$) than for limpets from all depredated populations (0.93 ± 0.04 , $n = 300$).

(b) Inaccessible limpets had a significantly lower SUI than accessible limpets at Malgas Island ($t = 3.16$, $P < 0.01$) and at Jutten Island ($t = 2.27$, $P < 0.05$), both islands with high densities of oystercatchers (respectively 60 and 63 birds per km of shore). Inaccessible limpets were not significantly different from accessible limpets at Cape Columbine ($t = 1.07$, $P > 0.1$), an area with lower oystercatcher density (two birds per km), although the trend was in the same direction. Overall, inaccessible limpets had a significantly lower SUI than accessible limpets ($t = 2.93$, $P < 0.01$).

(c) Limpets taken by oystercatchers had a significantly lower SUI than accessible limpets at Malgas Island ($t = 4.64$, $P < 0.001$), but at Jutten Island the difference was not significant ($t = 0.25$, $P > 0.1$) although the trend was

in the same direction. Densities of oystercatchers at the two sites are similarly high, but at Malgas Island, the proportion of *P. granularis* in the diet (36%) is greater than at Jutten Island (26%) (Hockey & Underhill, MS). Overall, limpets taken by oystercatchers had a lower SUI than all accessible limpets ($t = 3.49$, $P < 0.001$).

(d) Inaccessible limpets in depredated populations overall had a greater SUI than limpets in predator-free populations ($t = 2.32$, $P < 0.05$).

Patella granularis grows allometrically, shell height increasing faster than shell length (BRANCH, 1975), but SUI was not correlated with limpet size (Table 1), in predator-free populations ($r = 0.17$, $P > 0.1$), in all samples combined ($r = 0.45$, $P > 0.05$) or in the additional samples from Froggy Pond ($r = 0.12$, $P > 0.2$), so that variation in limpet size can be eliminated as a factor influencing SUIs. Similarly, wave action does not influence SUI. In both samples from Froggy Pond (one sheltered, one exposed) the mean SUI was 0.94 ± 0.03 .

DISCUSSION

The hypothesis that limpets in predator-free populations will be more pear-shaped than those in depredated populations was upheld. Similarly, the hypothesis that accessible limpets will be more elliptical than inaccessible limpets was supported in areas where the density of oystercatchers is high. At a low density site, Cape Columbine, the trend was the same but not significant.

The mean SUIs for inaccessible limpets and limpets consumed by oystercatchers were the same, but the former was significantly higher (*i.e.*, shells more elliptical) than the mean SUI for predator-free populations. This further supports the second hypothesis and implies that shell shape is, at least to some extent, genetically determined, and that predation by oystercatchers influences the limpet gene pool. If this were not the case, inaccessible and predator-free populations would have similar SUIs.

The possibility of a latitudinal influence on shell shape was considered, but Table 1 clearly illustrates that there is no trend in shape with decreasing latitude.

There are no other important vertebrate predators of *P. granularis*. Very small individuals are occasionally taken from mussel beds by Turnstones, *Arenaria interpres*, and Whitefronted Plovers, *Charadrius marginatus*; and the Giant Clingfish, *Chorisochismus dentex*, preys on limpets;

but *P. granularis* is a negligible component of the diets of these three species (STOBBS, 1980; BRANCH, 1981; personal observations).

From this we conclude that the selective influence by oystercatchers alone on the genotypes of *P. granularis* is sufficient to be detectable in the phenotypes.

ACKNOWLEDGMENTS

We thank John Cooper and Peter Ryan for collecting specimens in northern Namibia and the Sea Fisheries Research Institute for allowing access, and providing transport, to islands under their control. Financial support was provided by the South African National Committee for Oceanographic Research (SANCOR). Statistical assistance was provided by T. M. Crowe; R. Prÿs-Jones and A. R. Palmer provided valuable comment on earlier drafts of the manuscript.

LITERATURE CITED

- BRANCH, G. M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32: 179–188.
- BRANCH, G. M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. Oceanogr. Mar. Biol. Ann. Rev. 19:235–380.
- EBLING, F. J., J. A. KITCHING, L. MUNTZ & C. M. TAYLOR. 1964. The ecology of Lough Ine XIII. Experimental observations on the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. J. Anim. Ecol. 33:73–83.
- FRANK, P. W. 1982. Effects of winter feeding on limpets by Black Oystercatchers *Haematopus bachmani*. Ecology 63: 1352–1362.
- HARTWICK, E. B. 1981. Size gradients and shell polymorphism of limpets with consideration of the role of predation. Veliger 23:254–264.
- HOCKEY, P. A. R. 1981. Feeding techniques of the African Black Oystercatcher *Haematopus moquini*. In: J. Cooper (ed.), Proc. Symp. Birds of the Sea and Shore, Cape Town, 1979 (Cape Town: African Seabird Group). pp. 99–115.
- PALMER, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33:697–713.
- STOBBS, R. E. 1980. Feeding habits of the Giant Clingfish *Chorisochismus dentex*. S. Afr. J. Zool. 15:146–149.
- VERMEIJ, G. J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge. 332 pp.